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Is *Erica tetralix* abundance on wet heathlands controlled by nitrogen deposition or soil acidification?

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ABSTRACT

Erica tetralix is the key species on NW European wet heathlands, where it is often found to be the dominating plant species. Consequently, it is of considerable concern that the species has decreased significantly in cover from 28% to 18% over a six-year period. In order to understand the underlying causes, a structural equation modeling (SEM) approach was applied on ecological data from 1130 wet heathland plots. Both atmospheric N deposition and soil acidification were included in the SEM. The most important causal effect revealed by the SEM was a significant negative effect of N deposition on the cover of *E. tetralix*, whereas soil acidity tended to have a negative effect of relatively less importance. There was no significant effect of N deposition on soil pH, which indicates that there are no major indirect effects of N deposition on the cover of *E. tetralix* mediated by soil acidification.

1. Introduction

Erica tetralix is the key species on NW European wet heathlands, where it is often found to be the dominating plant species (EU, 2003). Consequently, it is of considerable concern that the species has decreased significantly in abundance from an average cover of 28%–18% across fifteen Danish wet heathland sites in the period from 2004 to 2009 (Bruus et al., 2010; Strandberg et al., 2011; Damgaard, 2012; Strandberg et al., 2012).

Different hypotheses for the causes of the observed decline in the abundance of *E. tetralix* on wet heathlands have previously been suggested by Strandberg et al. (2012),

i. An increased atmospheric N deposition for more than fifty years due to industrial combustion and husbandry has led to a gradual buildup of N in the soil, and the relatively easy access to N has allowed relatively nitrophilous plant species to outcompete *E. tetralix*. The hypothesis is weakly supported by the non-significant tendency of a relatively larger decline in the cover of *E. tetralix* at the sites with relatively high N deposition (Damgaard, 2012) and, generally, the effects of N deposition are perceived as one of the major causes of deterioration of nutrient poor terrestrial habitats (e.g. Bobbink et al., 2010). Growth stimulation caused by N deposition may affect the level of micronutrients used for plant growth, e.g. B and Mn as well as primary and secondary nutrients such as K and Mg (Hodges, 2010), resulting in less healthy plants that are more vulnerable to stress and competition by species with the ability to take up limiting nutrients for instance from deeper layers by having deeper roots than heathland shrubs.
ii. Acidification due to e.g. atmospheric N and S deposition and the management practice of regular burning have resulted in a critically low soil pH, which has led to reduced availability of base cations needed for growth or even toxic concentrations of Al- and Fe-ions in soil water and, consequently, increased mortality of *E. tetralix* during periods of environmental stress. This hypothesis is supported by the observed mortality pattern of *E. tetralix* in 2010, where several large monospecific patches of *E. tetralix* died at several wet heathlands sites (Strandberg et al., 2012). To illustrate this, liming experiments in acidified heathlands have resulted in restored base cation concentrations and an increase of pH (Dorland et al., 2005).

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iii. The abundance of *E. tetralix* in Denmark is controlled by the amount of accessible water, and often topography controls its distribution with typical dry heathland vegetation with *Calluna vulgaris* on crests and upper slopes, while wet heathlands are dominated by *E. tetralix*, *Trichophorum germanicum* (*Deergrass*) *and Molinia caerulea* (purple moor grass) on foot-slopes and valleys (Strandberg et al., 2012). Consequently, change in hydrology due to draining, water abstraction and/or changes in temperature and precipitation pattern is expected to have an effect on the distribution of the species.

iv. The climate in Denmark tends to become more extreme, i.e. prolonged drought periods in spring, increased precipitation in autumn and winter (Karlsson et al., 2010), and such climate changes may also affect the distribution range of *E. tetralix*, either by stressing it further where it is already stressed by some of the factors mentioned above or in peripheral areas of its distribution and isolated relict populations.

v. Other changes in management practices, such as cutting or a change in grazing regime and intensity may influence the cover of *E. tetralix* (Bullock and Pakeman, 1997) or the susceptibility to pathogens.

The above listed hypotheses are not mutually exclusive, and note that the effect of atmospheric N deposition on the cover of *E. tetralix* may be either direct through changing the amount of plant available N or indirect through soil acidification. Soil acidification has been studied intensively since the 1970s and 1980s (Ulrich et al., 1980; Breemen et al., 1984), when soil acidification was realized to be a widespread phenomenon in NW Europe and North America and an increasing threat to the wellbeing of forests. However, a comprehensive understanding of atmospheric deposition-soil acidification processes was first achieved in the 1980s (de Vries and Breeuwsma, 1986; Ugolini and Sletten, 1991; Driscoll et al., 2001). Research during the past two decades has particularly focused on the effects of soil acidification on forest health (e.g. Gundersen et al., 2006). Some studies have elucidated acidification effects on grassland (e.g. Stevens et al., 2009), while only few studies have been reported from heathland where plant—soil interactions on dry, coastal or alpine sites have been in focus (Bowman et al., 2008; Kleijn et al., 2008; De Graaf et al., 2009; Remke et al., 2009; Bobbink et al., 2010). The limited number of studies on non-calcareous heathland soils is likely related to the fact that these soils initially were considered so acidic that any further proton input would not significantly influence soil acidity. This despite the fact that such soils are formed on parent materials susceptible for changes in buffer systems (e.g. de Vries and Breeuwsma, 1986), especially if redox processes promote H^+ production in certain landscape positions where lateral subsurface flow accumulates precipitation. This situation is believed typical for wet heathland sites in Denmark, as well-developed pedogenic spodic horizons here impede water infiltration and promote lateral flow.

Studies from England and Wales indicate that neutral NW European surface soils have experienced a modest pH increase during the past two decades after a minimum pH around 1990, mainly due to the peak of atmospheric S deposition during this time (Kirk et al., 2010). In nitrogen addition experiments, Bowman et al. (2008) found that nitrogen decreased the biomass of vascular plants as well as the leaf concentration of calcium and magnesium in shoots and suggested that the site Tatra Mountains, Slovakia, and probably other sites too, have reached a new and potentially more toxic level of soil acidification in which aluminum release is superseded by iron release into soil water. Despite declining S inputs, soil acidification still seems to deteriorate susceptible soils with low buffering capacity (e.g. Blake et al., 1999), mainly as N deposition, and, hence, biogeochemical produced H^+ input rises or continues to be high (Bowman et al., 2008; Rice and Herman, 2012). A recent 10-years study from a wet heathland (peat bog) in Scotland revealed that dry (NH_3) and wet-deposition ($NH^{+}{}_4$ and NO_3^-) of 56 kg-N ha^{-1} yr^{-1} caused different soil water leaching chemistry and plant (*Calluna vulgaris*) and *Sphagnum* sp moss dieback patterns and that dry deposition has most adverse effects (Sheppard et al., 2013). For comparison, the annual average nitrogen deposition in Denmark ranges between 14 and 18 kg-N ha^{-1} yr^{-1} in the areas where wet heathland is most abundant (Ellermann et al., 2012). Locally the deposition can be significantly higher in places where pig breeding results in increased deposition of reduced nitrogen compounds. Hence, both the speciation and the deposited N form are important when decreasing plant species abundances should be evaluated.

Reported cases where plant nutrients have been shown to affect the species richness on nutrient poor heathlands adversely are by base cations, P and Mn availability, NH_4^+/NO_3^- ratios, and often combined with other stress factors as Al toxicity, water availability, grass competition or management (Kleijn et al., 2008). Recently, soil acidification due to high N deposition has even been shown to cause a change in soil buffering systems where both Ca and Al-silicate systems have been depleted and Fe-hydroxides buffering, normally only found in acid mine soils, are dominating (Bowman et al., 2008). The latter case is highly interesting in respect to the observed decline in *E. tetralix* abundance, although the Danish N deposition rates are considerably lower, as they reflect that base cation nutrient concentrations/availability (typically expressed by a Ca/Al ratio (e.g. Cronan and Grigal, 1995; Løkke et al., 1996)) are highly dependent on threshold pH (H_2O) values of ca. 4.5 for Al-toxicity and 3.5 for Fe-toxicity (Bowman et al., 2008), which in susceptible acid soil may be trespassed due to e.g. H^+ releasing redox processes after prolonged rain or management that removes base cations via biomass. Adverse plant stress in wet acid, nutrient poor heathlands are, thus, expected to be episodic in nature due to temporary elevated solution concentrations of Al and/or Fe.

In order to conserve the characteristic vegetation in nutrient-poor heathlands, they have been actively managed to reduce grass dominance and invasion of trees. This management has traditionally been implemented through biomass removal that resets the succession and removes nitrogen (Power et al., 1998; Power et al., 2001; Barker et al., 2004; Niemeyer et al., 2005). Typical methods for biomass removal include grazing, mowing, turf stripping and burning (e.g. Bokdam and Gleichman, 2000). Nowadays, most management is mechanized, resulting in the homogenization of the vegetation. It is expected that the occurrence of fires is considerably lower on wet than on dry heathland.

Heathlands are relatively simple ecosystems with few dominating higher plants, and this property makes it a relatively feasible task to model the ecological processes and, especially, the interaction between soil chemistry and plant population ecology. Recently, there has been a remarkable advance in the empirical modeling of ecological processes using Structural Equation Modeling (SEM) and state-space models that allow parameterizing complex models with many parameters and latent variables, and it has been demonstrated how the use of these modeling techniques provides unprecedented possibilities for detecting causal ecological relationships, testing compound ecological hypotheses, and making ecological predictions with quantitative estimates of the uncertainty that is associated with ecological predictions (e.g. Clark, 2007; Grace et al., 2010; Damgaard, 2011; Damgaard et al., 2011b; Grace et al., 2011). One thing that distinguishes SEM from most other current approaches to data modeling is its emphasis on estimating causal effects at the system level, and since it has a strong focus on the modeling of both direct and indirect causal